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Key Points:
- We report a novel relationship between seasonal photochemical reflectance index and sap flow in a mature conifer forest
- The photochemical reflectance index responded to seasonal water and energy limitations due to its association with photoprotection
- The photochemical reflectance index has remarkable potential as a proxy for forest functional response to seasonal ecohydrologic forcing

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The Photochemical Reflectance Index (PRI) Captures the Ecohydrologic Sensitivity of a Semiarid Mixed Conifer Forest

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Abstract At the seasonal time scale, daily photochemical reflectance index (PRI) measurements track changes in photoprotective pigment pools as plants respond to seasonally variable environmental conditions. As such, remotely sensed PRI products present opportunities to study seasonal processes in evergreen conifer forests, where complex vegetation dynamics are difficult to capture due to small annual changes in chlorophyll content or leaf structure. Because PRI is tied explicitly to short- and long-term changes in photoprotective pigments that are responsible for regulating stress, we hypothesize that PRI by extension could serve as a proxy for stomatal response to seasonally changing hydroclimate, assuming plant functional responses to stress covary in space and time. To test this, we characterized PRI in a semiarid, montane mixed conifer forest in the Madrean sky islands of Arizona, USA, during the monsoon growing season subject to precipitation pulse dynamics. To determine the sensitivity of PRI to ecohydrologic variability and associated changes in gross primary productivity (GPP), canopy spectral measurements were coupled with eddy covariance CO_2 flux and sap flow measurements. Seasonally, there was a significant relationship between PRI and sap flow velocity ($R^2 = 0.56$), and multiple linear regression analysis demonstrated a PRI response to dynamic water and energy limitations in this system. We conclude that PRI has potential to serve as a proxy for forest functional response to seasonal ecohydrologic forcing. The coordination between photoprotective pigments and seasonal stomatal regulation demonstrated here could aid characterization of vegetation response to future changes in hydroclimate at increasing spatial scales.

Plain Language Summary In order to understand how ecosystems interact with climate and how these relationships may change under future conditions, it is necessary to study how carbon and water move between plants and the atmosphere and how environmental stress, such as changing water availability, impacts these processes. For decades, satellites used in remote sensing studies have been able to measure how "green" an ecosystem is, but for forests that remain visibly green year-round even under stressful conditions, these greenness indices may not probe deeply enough beneath the surface to provide a clear picture of plant function. An alternative reflectance-based index, termed the photochemical reflectance index, or PRI, is able to detect seasonal changes in leaf pigments that are responsible for regulating plant stress. Here, we use tower-based PRI data from a semiarid conifer forest to show that variations in PRI correspond to the way in which plants regulate their water loss as moisture and temperature conditions change throughout the growing season. This result demonstrates that PRI is an effective indicator of how ecosystems respond to stressful environmental conditions, and therefore has the potential to advance our ability to distinguish how water availability influences forest productivity.

1. Introduction

Accurate modeling of coupled carbon (C) and water (H_2O) cycles is critical for understanding and predicting a wide range of feedbacks between climate and the terrestrial biosphere. In the western United States (USA), montane forests are important contributors to the region's C and H_2O exchange (Desai et al., 2011;

Knowles et al., 2020; Schimel et al., 2002). However, they are highly sensitive to changing temperature and water availability (Monson et al., 2002) and projected to experience severe increases in moisture stress (Williams et al., 2013). Therefore, early detection of forest stress response is critical for the monitoring and mitigation of negative impacts of intensifying droughts. Severe drought in recent years in the semiarid west has already led to widespread forest overstory mortality (Breshears et al., 2005). Yet a lack of robust methodology for measuring coupled C and H_2O fluxes on large spatial scales impedes the ability to model broad-scale forest response to environmental change. The southwestern USA is a natural setting for examining the influence of environmental drivers on the productivity of drought-affected forests (Seager et al., 2007; Udall & Overpeck, 2017), as well as evaluating the ability to track these relationships using optical methods. The Madrean sky island montane conifer forests in the southwestern USA, in particular, are warmer, more arid, and more dependent on summer rains than comparable forests to the north (Knowles et al., 2020). Therefore, these forests provide a unique opportunity to observe how coupled measures of ecosystem C and H_2O exchange are impacted by precipitation seasonality, which has important implications for future vegetation dynamics as western montane forests across latitudes are expected to experience increased aridity and changing hydrologic seasonality.

Net surface-atmosphere fluxes of C and H_2O can be quantified at the ecosystem level using eddy covariance (EC) flux towers (Baldocchi, 2008), and at the leaf level using chamber enclosure systems (Long & Bernacchi, 2003). While field methods at the leaf and canopy scale obtain irreplaceable mechanistic information, remote sensing methods provide estimates of terrestrial gross primary productivity (GPP) with extensive spatiotemporal coverage (Field et al., 1995; Jung et al., 2011; Prince & Goward, 1995; Running et al., 2004; D. Schimel et al., 2015; Smith et al., 2016). However, conventional global models based on satellite observations largely fail to capture the high degree of C and H_2O flux variability that is characteristic of semiarid ecosystems (Biederman et al., 2017), which are highly sensitive to precipitation inputs and climate anomalies (Scott et al., 2015). Therefore, improving the capability of remote sensing to monitor photosynthetic and stomatal response to hydrologic variability is needed.

In addition, traditional spectral-based vegetation indices, such as the normalized difference vegetation index (NDVI) or enhanced vegetation index (EVI), do not adequately reflect temporal changes in plant function in evergreen systems, where vegetation dynamics are not controlled by annual changes in chlorophyll content or leaf structure (Gamon et al., 1995; Magney et al., 2019; Smith et al., 2019; Walther et al., 2016; Wong et al., 2019). Rather, changes in light use efficiency (LUE) are controlled by a diverse suite of photoprotective processes working in concert (Björkman & Demmig-Adams, 1995), which may not influence green canopy display. When a plant absorbs radiant energy in excess of what it can use to drive electron transport, it must dissipate energy that would otherwise cause photo-oxidative damage (Barber & Andersson, 1992; Demmig-Adams & Adams, 2000). This energy dissipation occurs through a suite of mechanisms acting across temporal scales. Over short time spans, the primary pathway is through flexible nonphotochemical quenching (NPQ) driven largely by the xanthophyll cycle—where the interconversion of three xanthophyll pigments dissipates excess absorbed light energy in direct response to changes in both incident irradiation and environmental stress (Demmig-Adams & Adams, 1992, 1996, 2006; Muller et al., 2001; Porcar-Castell, 2011). In evergreen species this flexible NPQ dominates during the growing season (Ensminger et al., 2004). In response to prolonged environmental stress such as in overwintering conifers, sustained forms of NPQ, including changing pigment pools, overnight retention of zeaxanthin, photoinhibition and other xanthophyll-independent mechanisms, work to downregulate photosynthesis (Adams & Demmig-Adams, 1994; Verhoeven, 2014). On seasonal time scales, it is primarily changing carotenoid pigment pools—xanthophylls, lutein, α-carotene, and β-carotene—that regulate photosynthetic function in response to environmental stress such as heat and drought (Baquedano & Castillo, 2006; Haldimann et al., 2008). Therefore, carotenoid levels are related to photosynthetic activity across seasons, as has been shown previously in conifers (Gamon et al., 2016; Wong et al., 2019; Wong & Gamon, 2015b) and evergreen chaparral shrubs (Stylinski et al., 2002).

The deepoxidation of xanthophyll pigments reduces reflectance at 531 nm, forming the basis for the remotely sensed photochemical reflectance index (PRI) (Gamon et al., 1992; Gamon & Surfus, 1999; Penuelas et al., 1995). As such, PRI uses the normalized difference of reflectance at 531 nm and reflectance at 570 nm, which is largely insensitive to changes in the xanthophyll cycle (Gamon, 1993; Gamon et al., 1997; Penuelas et al., 1995). Therefore, in contrast to vegetation greenness indices that approximate the

photosynthetically active radiation (PAR) absorbed by the canopy (APAR) (Myneni & Williams, 1994), PRI has demonstrated ability to serve as a proxy for LUE over the short term (for reviews, see Garbulsky et al., 2011; C. Zhang et al., 2016), assuming xanthophyll cycle dynamics respond in concert with changes in LUE (Demmig-Adams et al., 2012). On the other hand, because both carotenoids and chlorophylls absorb at 531 nm, while chlorophylls but not carotenoids absorb at 570 nm, the relationship between PRI and LUE at the seasonal time scale is confounded by long-term changes in carotenoid to chlorophyll (Car/Chl) ratios (Garrity et al., 2011). There is substantial evidence that changing Car/Chl ratios dominates the seasonal PRI signal (Filella et al., 2009; Frechette et al., 2016; Gitelson et al., 2017; Hmimina et al., 2015; Porcar-Castell et al., 2012; Sims & Gamon, 2002; Stylinski et al., 2002; Wong et al., 2020; Wong & Gamon, 2015b). The PRI relationship with long-term changes in Car/Chl has been termed the "constitutive" component, while its relationship with short-term, reversible changes in the deepoxidation state (DEPS) of the xanthophyll cycle has been termed the "facultative" component (Gamon & Berry, 2012). That PRI is a composite of plant physiological and pigment adjustments complicates interpretation of its variability in response to environmental conditions on sub-weekly to subseasonal scales.

The amount of APAR used by chlorophyll for photochemistry depends on the physiological state of the plant (Papageorgiou & Govindjee, 2014), and the presence of any environmental stress can cause light energy to be absorbed in excess of that needed for C assimilation (Demmig-Adams et al., 2012). The PRI is therefore related to stress mediated reductions in photosynthesis operating on a time scale of minutes to days to months (Gamon & Berry, 2012). Accordingly, PRI has been shown to vary with changing environmental conditions, such as temperature (Dobrowski et al., 2005; Porcar-Castell et al., 2012), and a robust body of literature has shown how PRI responds to water stress (Evain et al., 2004; Filella et al., 2004; He et al., 2016; Inoue & Penuelas, 2006; Magney et al., 2016; Penuelas et al., 1998; Ripullone et al., 2011; Rossini et al., 2013; Soudani et al., 2014; Suarez et al., 2008; Sun et al., 2014; Thenot et al., 2002; Tsonev et al., 2014; Zhang et al., 2017; Zarco-Tejada et al., 2012). He et al., 2016 showed that in drier areas where both supply and demand of water interact to control productivity, using MODIS-based PRI as a proxy for water supply improved modeled estimates of GPP constrained by VPD alone, indicating that detection of seasonal changes in Chl/Car levels with remote sensing indices can be useful for studying soil moisture constraints.

The coupled exchange of CO_2 and H_2O is regulated at the leaf surface by stomatal control (Collatz et al., 1991; Meinzer, 2002), and this physiological regulation upscales to have significant impact on broad-scale C and H_2O cycling (Barron-Gafford et al., 2012; Bonan, 2008). Despite its critical importance, it is difficult to measure stomatal regulation at large spatial scales. As stomatal conductance declines, photosynthetic C fixation is limited by CO_2 diffusion into the leaves. In turn, photosystem II (PSII) activity is downregulated, and photoprotective processes coordinately upregulated in response to excess light (Verhoeven, 2014). Therefore, assuming the hypothesis of "functional convergence" (Field, 1991) or "coordinated regulation" (Gamon & Bond, 2013)—that plants coordinately regulate stomatal opening, CO_2 assimilation, PSII light harvesting, and photoprotective mechanisms—the PRI should be an indirect indicator of stomatal control and transpiration flux (Gamon et al., 1997), as has been demonstrated in crop (Suarez et al., 2008; Sun et al., 2014; Thenot et al., 2002; Zarco-Tejada et al., 2013), herbaceous (Verma et al., 2017), and deciduous systems (Hmimina et al., 2014; Naumann et al., 2010), as well as diurnally in conifers (Gamon & Bond, 2013). Additionally, Hilker et al. (2013) used stand level PRI in Canadian conifer forests as a remotely sensed proxy of LUE to successfully model transpiration and by extension stomatal conductance via the Ball-Berry-Collatz relationship. We expect the tight stomatal control of photosynthesis to be apparent seasonally in this semiarid, precipitation pulse system and that shifting carotenoid pigment pools measured with PRI will be coordinately regulated with GPP (Gamon et al., 2016; Wong et al., 2020) and transpiration flux across the growing season.

In a broader context, PRI's potential to provide important information about plant regulation of environmental stress means it could serve a complementary role in the development of other novel remotely sensed measures of GPP such as solar-induced fluorescence (SIF) (Cheng et al., 2013; Magney et al., 2019; Smith et al., 2018; Zuromski et al., 2018), a major goal of the European Space Agency's Fluorescence Explorer (FLEX) satellite program (Drusch et al., 2017) However, to advance its development, systematic in situ PRI acquisitions are needed in conjunction with ecosystem functional measurements (Gamon et al., 2010). One of the greatest barriers to a complete understanding of C and H_2O cycles is the difficulty in reconciling

estimates obtained across different spatiotemporal scales. The growing field of proximal remote sensing affords the unique opportunity to pair optical and flux measurements, in order to understand how ecophysiological mechanisms drive observed broad-scale ecosystem dynamics (Gamon, 2015; Shiklomanov et al., 2019). In this study, we measured PRI in conjunction with CO_2 and H_2O fluxes from a semiarid, montane mixed conifer forest, in order to characterize the use of PRI as a proxy for plant response to ecohydrologic constraints. Our primary objective was to determine the sensitivity of canopy scale PRI to (a) subseasonal climatic variability in a semiarid environment subject to monsoonal precipitation pulses, and (b) to monsoon season changes in GPP in a mature conifer forest. While a body of work in other geographic areas has reported on the seasonal relationship between carotenoid-based indices and photosynthetic function in conifers (Eitel et al., 2019; Frechette et al., 2016; Gamon et al., 2016; Porcar-Castell et al., 2012; Wong & Gamon, 2015a, 2020), the current study extends on previous work by analyzing how these relationships interact with the climate and ecohydrology of the semiarid southwestern United States.

2. Data and Methods

2.1. Study Site

The study location was a montane mixed conifer forest in the Coronado National Forest on Mt. Bigelow, northeast of Tucson, Arizona, USA. The site is at 2,573 m elevation in an area of significant topographical complexity. The climate is semiarid with a mean annual temperature of 9.4°C and mean annual evapotranspiration (744 mm) that exceeds precipitation (614 mm) (Knowles et al., 2020), approximately 50% of which falls during the North American Monsoon in late summer (Adams & Comrie, 1997). The site is dominated by mature second-growth Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and southwestern white pine (*Pinus strobiformis*), with little understory vegetation. The forest exhibits a bimodal pattern of primary production, with an initial spring peak following snow melt, a dry premonsoon midseason depression (May–June), and a secondary productivity peak during the wet monsoon (July–Sept), remaining active through fall and winter.

2.2. Eddy Covariance Fluxes

We used an EC flux tower to measure ecosystem-scale CO_2, water vapor, and energy fluxes. The 30 m tower (AmeriFlux site code US-MtB) has been in continuous operation since 2009 and is equipped with an open-path infrared gas analyzer (IRGA; LI-7500, Li-COR, Lincoln, NE, USA) and a three-dimensional sonic anemometer (CSAT 3, Campbell Scientific, Logan, UT, USA), in addition to sensors measuring PAR (LI-190, LI-COR, Lincoln, NE, USA) and air temperature (T_{air}) and relative humidity (HMP45C, Vaisala, Helsinki, Finland). Details on the tower structure and instrumentation can be found in Knowles et al. (2020). We used a light response curve methodology (Lasslop et al., 2010) to partition the net ecosystem exchange of CO_2 (NEE) into GPP and ecosystem respiration. We calculated LUE as GPP per unit PAR, due to a lack of robust estimate of APAR; however, changes in the fraction of absorbed PAR were minimal over the course of the study according to canopy measured as well as MODIS NDVI (data not shown).

2.3. Ecohydrologic Measurements

We measured sap flow on the north and south sides of three *P. strobiformis* and two *P. ponderosa* individuals using the thermal dissipation probe method (Granier, 1985, 1987). Data were logged at 30 min resolution using an upper heated probe and lower reference probe (TDP-30, Dynamax Inc., Houston, TX, USA) implanted in the sapwood of the tree approximately 40 mm apart. Sap flow velocity (cm hr^{-1}) was calculated according to

$$V_s = 0.0119K^{1.231} \times 3,600 \quad (1)$$

where

$$K = \frac{dTM - dT}{dT} \quad (2)$$

and dT is the difference in temperature (°C) between the two probes, and dTM is the maximum temperature difference between midnight and 7:00 a.m. In addition, we measured soil volumetric water content

(VWC) continuously using six water content reflectometers (CS-616; Campbell Scientific, Logan, UT, USA) buried at 5- and 15-cm depth beneath the soil surface to the east, north, and south of the tower.

2.4. Canopy Spectral Reflectance Measurements

On 3 July 2018, we installed an autonomous Spectral Reflectance Sensor (METER Group, Inc., Pullman, WA, USA), and began collecting PRI reflectance at 10-min intervals. For a complete description of the sensor see http://manuals.decagon.com/Manuals/14597_SRS_Web.pdf and Magney et al. (2016). The PRI sensors use photodiodes with narrow band-pass filters centered at the 532- and 570-nm wavelengths with 10 nm full width half maximum bandwidths. It uses a hemispherical upward-looking sensor, and a field stop downward-looking sensor to measure incoming and upwelling radiation (W m^{-2} sr^{-1} nm^{-1}), respectively. PRI was calculated as

$$PRI = \frac{\rho_{532} - \rho_{570}}{\rho_{532} + \rho_{570}} \quad (3)$$

where $\rho_{532}$is the spectral reflectance value at center wavelength of 532 nm and ρ_{570} is the spectral reflectance value at center wavelength of 570 nm. This calculation of PRI differs slightly from the original formulation that uses reflectance at center wavelength 531 nm; however, this formulation has been shown to work as both a seasonal and diurnal indicator of changing pigments (Gamon et al., 2015). Downward looking sensor interference filters restrict the field of view (FOV) to 36°. The sensor was mounted at 24 m height—roughly 12 m above the top of the canopy, and titled off-nadir at an angle of 20°, resulting in a field of view (FOV) of ~50 m^2. The PRI sensor faced west and therefore measured eastern facing needles. Within the sensor FOV were full or partial canopies of five trees (three *P. ponderosa* and two *P. strobiformis*, no understory vegetation), four of which were equipped with sap flow sensors.

We conducted a seasonal analysis during the monsoon season of July, August, and September 2018. We used only 10-min data where solar zenith angle minus sensor angle (20°) were less than 40° following Mottus et al. (2015), who found that geometry effects on canopy PRI were small for angles within this range. We summarized 10-min data into one daily value by taking the morning average (10:00–12:00 MST) for all data when PAR > 1,000 μmol m^{-2} s^{-1}. Because the sensor measured eastern facing needles, this time frame represents conditions with the highest Sun:shade illumination fraction, minimizing the effects of canopy shading caused by Sun angle (Hall et al., 2008; Hilker et al., 2008, 2010). Physical factors complicate the acquisition of canopy scale diurnal PRI, including sun sensor geometry effects on illumination (Barton & North, 2001; Grace et al., 2007; Hall et al., 2008; Hilker et al., 2008), mixed-pixel background effects, and canopy structural effects (Hernandez-Clemente et al., 2011, 2016; Jia et al., 2018). These complicating effects can decouple canopy PRI from leaf physiology. While the data obtained with this single sensor is not robust enough to thoroughly account for canopy structure complexities, the selection of this time frame follows previous studies that observed that the highest correlations between PRI and LUE occur under clear sky conditions and for sunlit canopy surfaces (Gamon et al., 1997; Hall et al., 2008; Soudani et al., 2014), and that on clear summer days, PRI of sunlit leaves is not strongly affected by Sun angle in conifer canopies (Middleton et al., 2009). We note that with this approach, the proportion of sunlit needles observed by the sensor may not be representative of the proportion within the entire EC flux footprint. However, in such a high light environment, we assume a large portion of the canopy is light saturated throughout much of the day (see Figure 3), with daily average PAR > 1,200 μmol m^{-2} s^{-1} from 8:30–15:00 MST.

2.5. Combined Gas Exchange and Fluorescence Leaf-Scale Measurements

To characterize the physiological and photoprotective status of needles during a particularly stressful time during the growing season, diurnal changes in needle function were analyzed with simultaneous gas exchange and chlorophyll fluorescence measurements at the leaf-scale. We collected data on 13–14 September on attached top of canopy needles (13-m height) using a canopy access crane; the difficulty of canopy access precluded the repetition of this sampling multiple times throughout the season. The sampled period corresponded to a midseason drop in GPP following the monsoon season peak productivity, and corresponded to a period of decreased water availability and minimum photosynthetic activity throughout the study period (see yellow shaded bar on Figure 1). We measured one tree of each species for *P. ponderosa* and one *P. strobiformis*. Measured trees were not located directly beneath the PRI sensor, so as not to disturb the

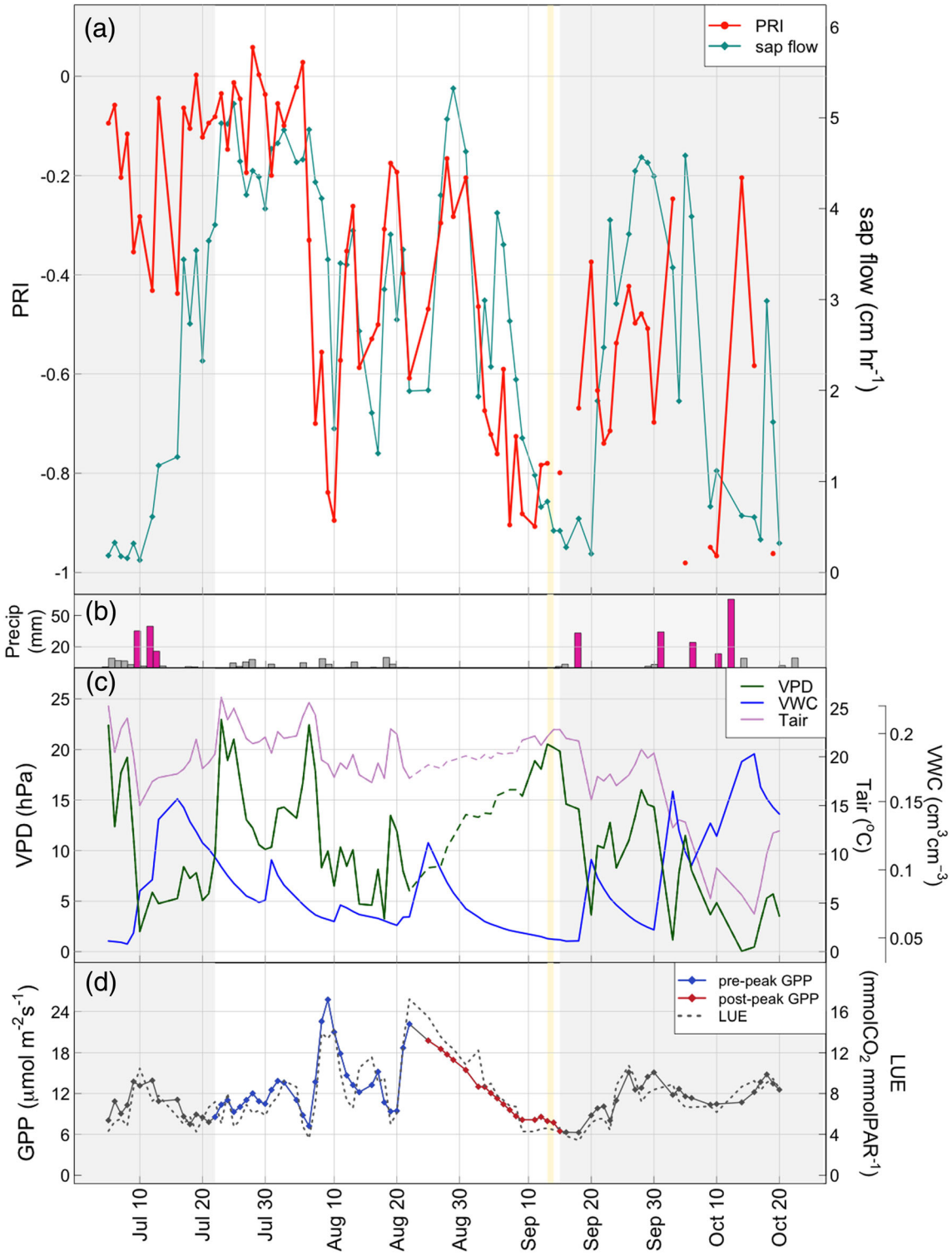

Figure 1. The seasonal evolution of daily average (a) PRI and sap flow velocity (b) daily summed precipitation, with precipitation events >10 mm highlighted in pink, (c) VPD, T_{air}, (dashed lines indicate gap-filled data), and VWC, and (d) GPP and LUE with prepeak GPP shown in blue, and postpeak GPP shown in red (corresponding to Figures 2b and 2d). Leaf level sampling in mid-September is highlighted with the yellow band. Periods exhibiting a time lag between PRI and sap flow are highlighted with gray shaded bands and were excluded from sap flow correlation analyses.

signal; however, they were adjacent to and of the same size, age class, and topographic position. We measured four branches on each tree every hour from 9:00–16:00 MST. On each branch, two sunlit fascicles (20 needles for *P. strobiformis* and 12 needles for *P. ponderosa*) were measured for simultaneous gas exchange and fluorescence. When measuring under intermittent cloudiness, measurements were aborted if the needles were not exposed to sunlight immediately prior to clamping the needles. Branch data under clear sky conditions were aggregated for each species, such that each hourly data point represents an average measurement of four branches. However, due to removal of cloudy sky data, three of the 13 hourly data points were averaged from three branches, three were averaged from two branches, and one consisted of a single branch measurement (see Figure 3f).

Gas exchange and simultaneous chlorophyll fluorescence were measured using the Li-6,800 Portable Photosynthesis System infrared gas analyzer (LICOR Inc., Lincoln, NE, USA) with a standard 6-cm^2 leaf chamber. Instantaneous measurements were taken to obtain net photosynthesis (A_{net}) and stomatal conductance to water vapor (g_{sw}). Following established methodology for these species in this ecosystem, we characterized ambient PAR, T_{air}, and relative humidity and set internal chamber conditions to approximate this ambient environment for each round of branch measurements (Potts et al., 2017). We performed leaf area analysis on 10 samples of each species to derive an average leaf area within the chamber (2.24 $cm^2 \pm 0.16$ cm^2 and 2.22 $cm^2 \pm 0.22$ cm^2 for *P. ponderosa* and *P. strobiformis*, respectively) assuming each sample clamped the same approximate amount of leaf area. Pulse amplitude modulated (PAM) fluorescence was used to obtain the quantum yield of photosystem II (ΦPSII), NPQ, and maximal photochemical efficiency of photosystem II (Fv/Fm) according to (Bilger & Bjorkman, 1990; Genty et al., 1989). We used the multiphase flash method to obtain greater accuracy in F_m' acquisition compared to typical rectangular flash methods (Loriaux et al., 2013). To obtain dark adapted parameters, rectangular flash measurements were taken at predawn on 14 September for a minimum of eight samples per branch to obtain branch averaged F_o and F_m. Prior to the study, we tested and determined that both the optimum red target parameter of the daytime multiphase flash method and optimum flash intensity of the predawn rectangular method for both species at this site was 8,000 μmol m^2 s^{-1}.

3. Results and Discussion

3.1. Seasonal PRI Responds to Ecohydrologic Dynamics

A key finding of our study was that PRI and sap flow varied in synchrony over the monsoon season ($R^2 = 0.56$, $p < 0.001$; Figures 1a and 2a). This result suggests that (1) PRI is capturing seasonal dynamics of photoprotection and photosynthetic downregulation and (2) sap flow and transpiration rates are related to photosynthetic inhibition due to their joint regulation by stomatal conductance (Collatz et al., 1991; Meinzer, 2002). However, the influence of precipitation pulses in semiarid ecosystems can cause functional parameters to decouple over relatively short time scales (Huxman et al., 2004). Sap flow response exhibited a ~2 day lagged response behind PRI during rain events with extremely low vapor pressure deficit (VPD) (Figures 1a–1c). During these times evaporative demand is too low to drive the physical pull of water, yet leaves are relieved of stress, resulting in a PRI response to unstressed conditions and sap flow following only after the water potential gradient is reestablished. In contrast, Zarco-Tejada et al. (2012) reported the opposite time delay, with PRI responding slightly behind $T_{canopy} - T_{air}$ during drought recovery after re-watering treatments. An important distinction is that our natural study system experienced rewatering due to rain events, which simultaneously affected the VPD and radiation intensity of the system, whereas their system experienced rewetting from irrigation independent of atmospheric conditions. Although time periods exhibiting this lag are shown with gray shaded bands in Figure 1, all subsequent analyses exclude these lag periods for consistency and are limited to the period from late July through mid-September (22 July to 15 September). During this time, PRI and sap flow were positively correlated ($R^2 = 0.56$, $p < 0.001$, Figure 2a).

While a number of studies in crop systems have demonstrated the link between seasonal PRI and measures or proxies of plant hydraulics (Magney et al., 2016; Rossini et al., 2013; Sarlikioti et al., 2010; Suarez et al., 2008; Zarco-Tejada et al., 2012), or shown that PRI is a good indicator of leaf water status (Ripullone et al., 2011; Sun et al., 2014), few have attempted to relate PRI to sap flow rates (Manzanera et al., 2017; Marino et al., 2014); although PRI has been shown to vary with a proxy for transpiration

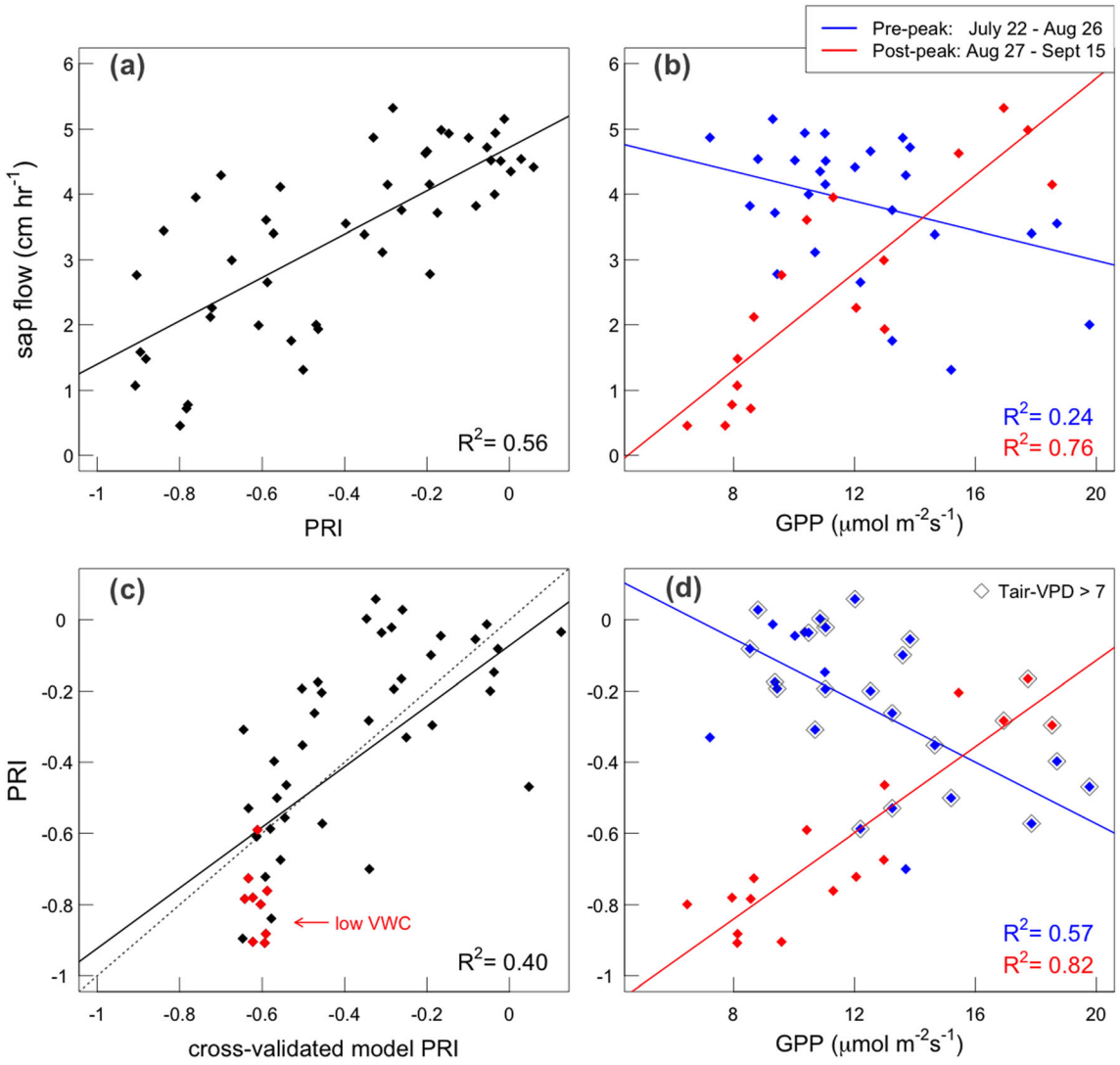

Figure 2. Regression analysis from 22 July to 15 September for daily average (a) sap flow and PRI; (b) sap flow and GPP; (c) observed PRI and PRI modeled from the cross-validated MLR using T_{air} and VWC (mid-September minimum VWC shown in red, and gray line represents 1:1); and (d) PRI and GPP (points where T_{air}-VPD > 7 are outlined in gray). For the GPP relationships, regressions are shown for prepeak GPP (blue) and postpeak GPP (red) time periods (corresponding with Figure 1d).

($T_{air} - T_{leaf}$) in crop systems (Rossini et al., 2013; Suarez et al., 2008). Our results agree with Marino et al. (2014) who showed a linear relationship between sap flux density and leaf-level PRI in olive trees ($R^2 = 0.42$), and Manzanera et al. (2017) who showed significant correlation between sap flow rate and single-tree PRI ($R^2 = 0.62$) in juvenile potted pines. We build upon these previous efforts by reporting for the first time, to our knowledge, a relationship between PRI and sap flow in a natural mature forest using novel canopy measurements of seasonal PRI at daily resolution. As Magney et al. (2016) reported on a diurnal scale in wheat, we demonstrate that seasonal stomatal opening is regulated similarly as PRI, supporting the hypothesis of coordinate regulation. This is not necessarily to say that stomatal control is associated with enzymatically triggered xanthophyll conversion or carotenoid pigment pool shifts in any direct sense, yet we do expect plant functional responses to stress to covary in space and time. Our data show that the separate mechanisms of stress response, stomatal control vs. pigment related photoprotection, appear to respond to environmental drivers in synchrony. While the mechanisms of photosynthetic regulation are well studied as individual components (Avenson et al., 2004; Flexas et al., 2004; Genty et al., 1989; Harbinson et al., 1990; Jahns & Holzwarth, 2012), it is challenging to

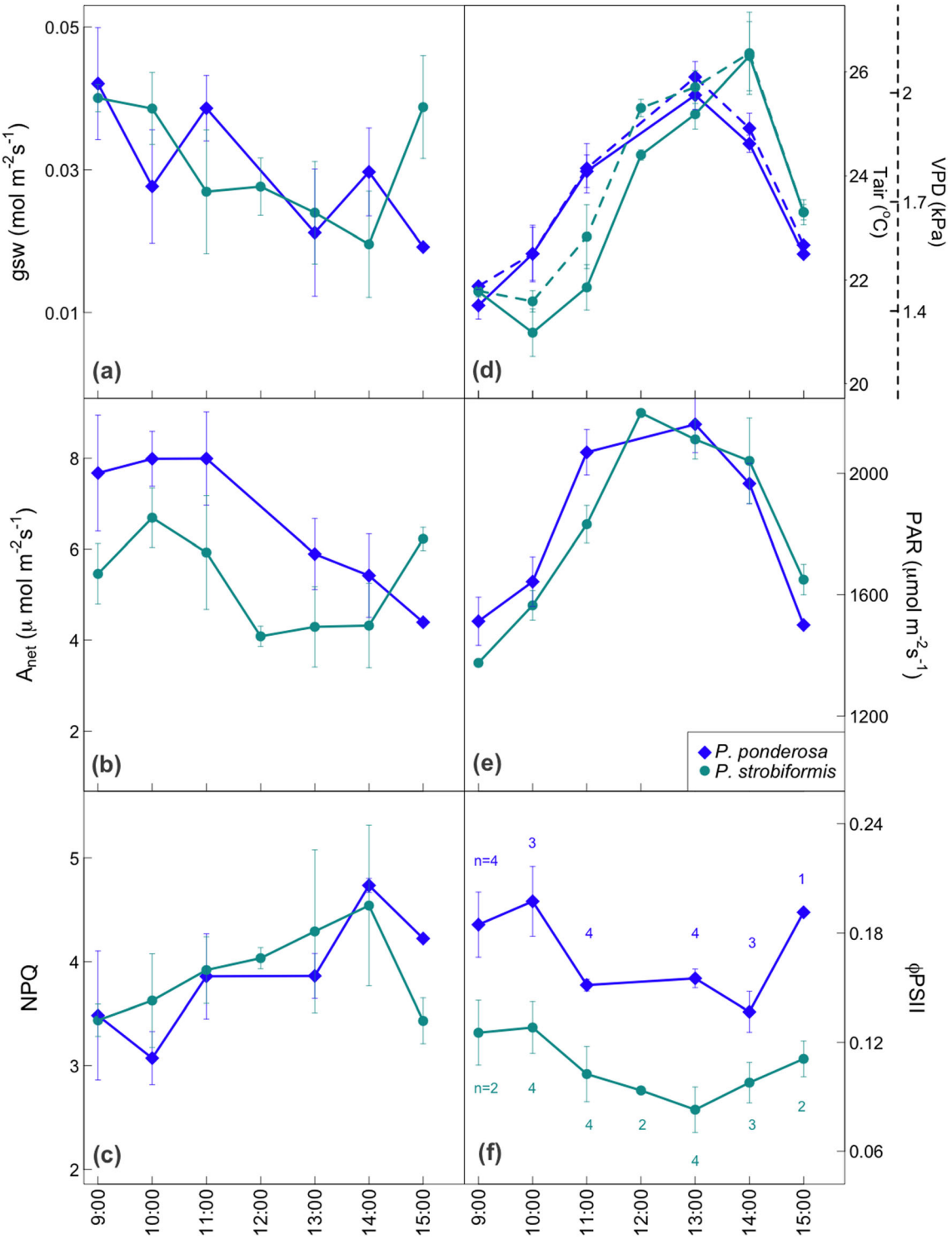

Figure 3. Leaf level hourly diurnal data for (a) g_{sw}, (b) A_{net}, (c) NPQ, (d) T_{air} (solid lines) and VPD (dotted lines), (e) PAR, and (f) ϕPSII. After removing some data due to cloudiness, each point is an average of 1–4 branch measurement shown by the number next to each point in Figure 3f. each branch measurement was a measurement of 20 needles for *P. strobiformis* (green) and 12 needles for *P. ponderosa* (blue). Error bars represent ±1SE from the mean. This sampling was concurrent with a drop in GPP and VWC following a dry spell on 13–14 September: Environmental conditions of these dates are shown with yellow highlight in Figure 1.

demonstrate regulatory processes occurring in coordination under field settings. Additional field studies which include seasonal variation in pigment concentrations are warranted to clarify the regulatory mechanisms connecting PRI and stomatal regulation of transpiration flux. Nonetheless, these sap flow results suggest that PRI is an effective indicator of forest response to ecohydrologic variability on a seasonal scale.

A connection between PRI and hydrologic variability was supported by our result that daily average PRI paralleled a combination of VWC ($p < 0.001$, $R^2 = 0.17$) and T_{air} ($p < 0.01$, $R^2 = 0.10$) throughout the monsoon season (Figures 1a and 1c); daily PRI was not significantly correlated with VPD or PAR. To investigate further, we performed a regression tree analysis (using the recursive partitioning package rpart in R Version 4.1–13) on the environmental drivers of PRI (Breiman et al., 1984): T_{air}, VWC, VPD, and PAR had variable importances of 37%, 29%, 27%, and 7%, respectively. Multiple linear regression (MLR) using VWC and T_{air} significantly predicted daily PRI ($R^2 = 0.52$, $p < 0.001$; $-2.1003 + 6.3295 * \text{VWC} + 0.0595 * T_{air}$). Cross-validation analysis, in which the model was trained with 70% of the data, tested on the remaining 30%, and iterated fivefold, produced a $R^2 = 0.40$ ($p < 0.001$, Figures 2b and 2c).

While previous studies have found PRI to vary seasonally in response to T_{air} in Japanese larch (Nakaji et al., 2006) and potted conifers exposed to a boreal climate (Wong & Gamon, 2015a), PRI has also been shown to be uncorrelated with T_{air} for evergreen needleleaf sites across the continental United States (He et al., 2016), and only weakly correlated with T_{air} in a subtropical conifer forest (Zhang et al., 2015). These inconsistencies may reflect varying degrees of temperature limitation and/or stress across diverse ecosystems. In addition, studies have shown that soil moisture can affect the PRI relationship with LUE (Inoue & Penuelas, 2006; Sims et al., 2006; Soudani et al., 2014) or irradiation (Magney et al., 2016), and these effects become stronger as soil moisture becomes increasingly limited. The demonstrated correlation between PRI and VWC in the current study supports previous work which showed that PRI was driven by a response to reduced soil moisture in wildland species (Hmimina et al., 2014; Merlier et al., 2015; Nestola et al., 2018; Zhang et al., 2017) and in crops (Inoue & Penuelas, 2006; Magney et al., 2016; Sarlikioti et al., 2010; Suarez et al., 2008; Sun et al., 2014). In fact, the MLR model performed the weakest during mid-September when VWC was extremely low (see red points in Figure 2c and see Figure 1c), and PRI may have been increasingly driven by water availability alone (see red dots in Figure 2c). This effect highlights that the relative strengths of T_{air} and VWC as environmental drivers are dynamic through time and likely complicated by threshold-type responses that are ecosystem specific and difficult to predict, making simple relationships between PRI and environmental variables elusive.

If PRI was driven by flexible xanthophyll dynamics, we would expect PRI to respond strongly to excess PAR; however, adding PAR into the MLR model resulted in no improvements. Possible explanations for this include light saturation and little variability in PRI (Sims et al., 2005), or that seasonal PRI as measured here is capturing changing carotenoid pigment pools ("constitutive pools") and is not primarily driven by the flexible xanthophyll cycle. This latter suggestion is likely given the consensus in the literature that the constitutive component of the PRI signal dominates at the seasonal scale (Wong & Gamon, 2015a). However, this study was conducted on a daily time step within a single season and did not encompass any clear seasonal transitions. PRI closely tracked day-to-day transpiration measured by sap flow during the monsoon growing season, and responded to sudden drops in T_{air} and precipitation pulse dynamics of VWC. One might expect that these rapid dynamic changes in response to hydrologic variables occur on shorter time scales than carotenoid pigment pool shifts measured with PRI; however, Sun et al. (2014) showed that the Car/Chl ratio was responsive to water availability and increased following rewatering in olive trees. Accordingly, this semiarid forest that is adapted to precipitation pulse dynamics may have the ability to increase sustained zeaxanthin or other carotenoid pigment pools many times throughout the year. Given that fully deconvolving the facultative and constitutive components of PRI was not possible with our data set, we hypothesize that changes in PRI that track the hydrologic variability of this system is driven by both flexible xanthophyll cycle DEPS in the short term (subweekly), as well as changing carotenoid pigment pools over the longer (subseasonal) time scale. Future studies in this system should focus on relating seasonal PRI to pigment data to investigate these hypotheses. Analysis of long-term (9-year) EC records at this site indicates that the forest, which experiences significant inter-annual climatic variability, can be both water and/or energy limited depending on the prevailing and antecedent conditions (Knowles et al., 2020). Taken together, our result that PRI was driven by a combination of VWC and T_{air} supports this conclusion, and indicates that PRI,

in responding to excess light (Björkman & Demmig-Adams, 1995), is able to integrate across ecosystem response to multiple environmental drivers.

3.2. Inconsistent PRI-GPP Seasonal Relationships

While many studies have attempted to relate PRI to canopy level productivity using flux data, results from the literature are inconclusive and a strong relationship between PRI and LUE may (Cheng et al., 2013; Louis et al., 2005; Nichol et al., 2002; Serrano & Penuelas, 2005) or may not be observed (Filella et al., 2004; Nakaji et al., 2006; Rahimzadeh-Bajgiran et al., 2012; Soudani et al., 2014). In this natural conifer system, PRI was not an effective indicator of GPP despite its strong response to environmental conditions. Pooled over the course of the entire study period, PRI and GPP were not statistically related ($p > 0.05$, Figure 2d, regression not shown). Instead, we identified an inconsistent relationship between PRI and GPP through time (Figure 1d). Specifically, there was a negative relationship between PRI and GPP prior to the GPP seasonal peak in late August ($R^2 = 0.57$, $p < 0.001$, Figure 2c), and a positive relationship after peak productivity ($R^2 = 0.82$, $p < 0.001$, Figure 2d); hereafter referred to as the prepeak (22 July to 26 August) and postpeak (27 August to 15 September) periods. The seasonal course of LUE was very similar to GPP (Figure 1d). Only a few seasonal PRI studies have been conducted in forests that experience a monsoon climate, and those have also reported inconsistent and weak relationships with estimates of productivity (Nakaji et al., 2006, 2014; Q. Zhang et al., 2015). In our system, the inverse PRI-LUE relationship in our system occurs during the period leading up to the second annual peak in productivity (monsoon peak as opposed to spring peak), and therefore cannot be explained by any obvious state change such as spring onset or senescence. We present three possible explanations for this observation:

1. Changing hydrologic variability. July and August mark the beginning and peak of the monsoon season and experience an overall wetter and more hydrologically variable environment relative to September (Figures 1b and 1c). In contrast to PRI, regression tree analysis for the environmental drivers of GPP showed that VPD rather than T_{air} ranked highest in importance. These results indicate that a divergence between T_{air} and VPD (i.e., when its humid) could decouple the PRI-GPP relationship. Indeed, there was a strong negative relationship between GPP and PRI when T_{air}-VPD > 7 ($R^2 = 0.57$, $p < 0.001$), and 88% of those points occurred during the prepeak period (Figure 2d), which experienced higher frequency monsoon convective storms and more variable atmospheric demand (Figure 1b and 1c). This suggests that it may be these times that are driving the negative pre-peak PRI-GPP relationship, and periods of high-frequency rain events and frequent alternations between sunny and cloudy conditions have been linked to scattered relationships between PRI and LUE (Soudani et al., 2014; Zhang et al., 2015). Zhang et al. (2015) determined significant negative PRI-LUE relationships around days with heavy precipitation events in a subtropical conifer forest, with PRI and LUE being correlated on 40% of dry season days but only 22% of rainy season days.
2. Seasonal decoupling in the PRI-GPP relationship may be driven by physiological mechanisms. When seasonal photosynthetic activity is regulated by changing Car/Chl ratios in response to changing environmental stress, the seasonal relationship between PRI and LUE may be magnified (Gamon & Berry, 2012; Wong & Gamon, 2015a). However, when photosynthesis is decoupled from the timing of these pigment pool changes, there can be a concurrent decoupling in the seasonal PRI-LUE relationship (Frechette et al., 2015, 2016; Porcar-Castell et al., 2012). It is possible that the observed decoupling between PRI and GPP represents a shift in pigment pool composition but that the shift in pigment pools does not necessarily correspond to GPP. Most commonly, examples of this decoupling are reported during seasonal transition periods (i.e., from winter to spring); however, at this site, which can remain photosynthetically active year-round, seasonal transitions are less distinct. We might expect sustained forms of NPQ to dominate during the prolonged premonsoon drought, when pigment pool adjustments following the start of the monsoon rewetting in early July may be decoupled from photosynthetic recovery. Although quantifying complete pigment pools was beyond the scope of this study, future work could analyze PRI data throughout the year in conjunction with a seasonal pigment composition to test this hypothesis.
3. A footprint mismatch between the PRI and GPP measurements is likely complicating interpretation of the seasonal relationship. PRI tracked sap flow throughout the 3-month study period, whereas GPP did not (Figures 1a, 1d, 2a, and 2b). During pre-peak when the PRI versus GPP relationship was

negative (Figure 2d), GPP and sap flow also demonstrated a weak negative relationship ($p < 0.01$, $R^2 = 0.24$; Figure 2b). In contrast, during postpeak when the PRI vs GPP relationship was positive (Figure 2d), GPP and sap flow were also positively correlated ($p < 0.001$, $R^2 = 0.76$; Figure 2b). Given that PRI is expected to relate to g_{sw} when diffusional limitations cause photosynthetic inhibition, PRI should be related to CO_2 assimilation when it is related to transpiration, contrary to our results. We attribute this discrepancy to a spatiotemporal mismatch between optical and flux methods (Gamon et al., 2006, 2010, 2015; Pacheco-Labrador et al., 2017). The size of any flux tower footprint varies with atmospheric stability (Chen et al., 2009), while spatial variability of PRI has been shown to be affected by species (Atherton et al. 2017; Guo & Trotter, 2004), and the species within the SRS sensor FOV are not fully representative of the demography within the entire flux tower footprint, as it excludes *P. menziesii*. Although the statistical flux footprint was seasonally consistent, and 80% of CO_2 flux originated from within approximately 500 horizontal meters upwind of the tower (Knowles et al., 2020), the cooccurrence of the negative PRI-GPP relationship with monsoon convective storms indicates that footprint variability complicated the relationship between EC measurements and optical data across changing hydroclimatic conditions. Conversely, the PRI sensor measured the full or partial canopy of only five trees, four of which were used to measure sap flow. Therefore, the spatial scales of PRI and sap flow measurements were nearly identical, which was likely conducive to tighter correlation between PRI and sap flow, as opposed to GPP.

3.3. Leaf Photoprotective State

The assumption of "coordinated regulation" forms the basis for a linkage between sap flow and PRI (Gamon & Bond, 2013). The current study incorporated top-of-canopy leaf level diurnal analysis to probe more deeply into the coordinated regulation and photoprotective status of the needles. Stomatal conductance and net carbon assimilation both responded to diurnal changes in VPD and T_{air}, with maximum values in the morning, followed by a midday depression, and a declining trend in the afternoon (Figures 3a, 3b, and 3d). Notably, NPQ was remarkably high by early morning, with values in excess of three by 9:00 am, and remained high throughout the day (Figure 3c). High NPQ values were supported by correspondingly low ΦPSII values (less than 0.2), that exhibited little variation (Figure 3f). That *P. strobiformis* appeared to have higher NPQ and lower ΦPSII resulting in lower A_{net}, indicates that this species was experiencing a higher degree of stress-induced reductions in photosynthetic function compared to *P. ponderosa*.

The fact that both PAR and NPQ were very high by early morning, while ΦPSII was quite low (Figure 3c, 3d, and 3f), indicates that these top-of-canopy needles exist in a state of maximum photoprotection throughout the entire day. This suggests that during this time period, leaves were subject to persistent light saturation, and PAR values show that the system exists in a state of extremely high irradiance (>1,200 μmol m^{-2} s^{-1}) throughout much of the day (8:30–15:00). ΦPSII and NPQ data suggest that the needles were already downregulated by early morning, providing additional evidence that flexible xanthophyll conversion is not the driving mechanism behind PRI during this time period. Although temporally limited, our leaf level physiological analysis provides supports that seasonally changing constitutive photoprotection, rather than diurnal facultative energy dissipation, dominated the PRI signal.

3.4. Future Directions

Few PRI studies have been conducted in systems that exhibit a bimodal production maxima, or in the semiarid conifer forests of the southwest USA. Following these results, future work that repeated our analysis multiple times throughout the season, paying particular attention to the transition between the premonsoon drought and monsoon rewetting periods, would be useful to constrain how seasonal dynamics may differ between the spring snowmelt production peak, and the summer monsoon production peak. Biochemical characterization of total pigment pools and the DEPS of the xanthophyll cycle could be evaluated in parallel throughout the year to discern whether PRI is representing facultative xanthophyll cycle activity versus constitutive pigment pool changes. Additionally, seasonally iterated leaf-scale analysis should be performed multiple times throughout each season using higher sample sizes to reduce the effects of leaf-leaf heterogeneity. This type of future analysis is recommended to untangle the mechanistic controls over the seasonality of PRI and its relationship to stomatal control under highly dynamic changes in water availability. Previous studies have found that the relationship between PRI and LUE breaks down during extreme drought (Guarini et al., 2014; Sims et al., 2006; Soudani et al., 2014; Tsonev et al., 2014), suggesting that the sensitivity of PRI to water availability may have a threshold that was not seen in the monsoon season of this study.

Therefore, extending these analyses into the premonsoon dry season would contribute to an understanding of a PRI threshold response to drought. From the results of the current analysis, we hypothesize that complex temporal phase decoupling may occur between PRI, transpiration, GPP, and pigment composition during seasonal transitions. Collectively, PRI in combination with complementary indices including SIF, the Chlorophyll Carotenoid Index (CCI) (Gamon et al., 2016), and thermal imagery may be necessary to disentangle coupled C and H_2O dynamics in this highly variable ecosystem.

4. Conclusions

In this study, we measured the photochemical reflectance index (PRI) in conjunction with GPP and transpiration fluxes from a semiarid, subalpine mixed conifer forest, in order to characterize the use of PRI as a proxy for plant response to the ecohydrologic variability of the monsoon season. The PRI responded to ecohydrologic dynamics as expected in a system that is characterized by both water and energy limitation, and we report for the first time a relationship between seasonal PRI and sap flow in a natural, mature forest. Although PRI responded to environmental conditions similarly to what we might expect from photoprotective pigments, PRI was not an effective indicator of GPP in this system. That the relationship between PRI and GPP changed over the course of the monsoon season was most likely affected by a footprint mismatch between the EC flux and optical data, but may also be influenced by changing hydrologic conditions associated with monsoon rain events and/or seasonally shifting pigment pools. This study demonstrates that PRI has remarkable potential to serve as a proxy for forest functional response to seasonal ecohydrologic forcing by extension of its association with photoprotection. Therefore, PRI could provide a means with which to monitor stomatal regulation at large spatial scales and characterize plant response to future changes in hydroclimate. We anticipate that these results will have implications for the use of remote sensing in the future, as projected wetter summers and warmer autumns of more northernly forests may resemble the monsoon season of this Madrean sky island ecosystem.

Data Availability Statement

The data sets used in the current study are available in the Dryad data repository (https://doi.org/10.5061/dryad.b2rbnzs9k).

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References

Adams, D. K., & Comrie, A. C. (1997). The North American monsoon. *Bulletin of the American Meteorological Society*, *78*(10), 2197–2213. https://doi.org/10.1175/1520-0477(1997)078<2197:TNAM>2.0.CO;2

Adams, W. W., & Demmig-Adams, B. (1994). Carotenoid composition and down regulation of photosystem II in three conifer species during the winter. *Physiologia Plantarum*, *92*(3), 451–458. https://doi.org/10.1111/j.1399-3054.1994.tb08835.x

Atherton, J., Olascoaga, B., Alonso, L., & Porcar-Castell, A. (2017). Spatial variation of leaf optical properties in a boreal forest Is Influenced by species and light environment. *Frontiers in Plant Science*, *8*. https://doi.org/10.3389/fpls.2017.00309

Avenson, T. J., Cruz, J. A., & Kramer, D. M. (2004). Modulation of energy-dependent quenching of excitons in antennae of higher plants. *Proceedings of the National Academy of Sciences*, *101*(15), 5530–5535. https://doi.org/10.1073/pnas.0401269101

Baldocchi, D. (2008). Breathing of the terrestrial biosphere: Lessons learned from a global network of carbon dioxide flux measurement systems. *Australian Journal of Botany*, *56*(1), 1–26. https://doi.org/10.1071/bt07151

Baquedano, F. J., & Castillo, F. J. (2006). Comparative ecophysiological effects of drought on seedlings of the Mediterranean water-saver *Pinus halepensis* and water-spenders *Quercus coccifera* and *Quercus ilex*. *Trees*, *20*(6), 689. https://doi.org/10.1007/s00468-006-0084-0

Barber, J., & Andersson, B. (1992). Too much of a good thing—Light can be bad for photosynthesis. *Trends in Biochemical Sciences*, *17*(2), 61–66. https://doi.org/10.1016/0968-0004(92)90503-2

Barron-Gafford, G. A., Scott, R. L., Jenerette, G. D., Hamerlynck, E. P., & Huxman, T. E. (2012). Temperature and precipitation controls over leaf- and ecosystem-level CO_2 flux along a woody plant encroachment gradient. *Global Change Biology*, *18*(4), 1389–1400.

Barton, C. V. M., & North, P. R. J. (2001). Remote sensing of canopy light use efficiency using the photochemical reflectance index - model and sensitivity analysis. *Remote Sensing of Environment*, *78*(3), 264–273. https://doi.org/10.1016/s0034-4257(01)00224-3

Biederman, J. A., Scott, R. L., Bell, T. W., Bowling, D. R., Dore, S., Garatuza-Payan, J., et al. (2017). CO_2 exchange and evapotranspiration across dryland ecosystems of southwestern North America. *Global Change Biology*, *23*(10), 4204–4221. https://doi.org/10.1111/gcb.13686

Bilger, W., & Bjorkman, O. (1990). Role of the xanthophyll cycle in photoprotection elucidated by measurements of light-induced absorbency changes, fluorescence and photosynthesis in leaves of *hedera canariensis*. *Photosynthesis Research*, *25*(3), 173–185. https://doi.org/10.1007/BF00033159

Björkman, O., & Demmig-Adams, B. (1995). Regulation of photosynthetic light energy capture, conversion, and dissipation in leaves of higher plants. In E.-D. Schulze, & M. M. Caldwell (Eds.), *Ecophysiology of Photosynthesis* (pp. 17–47). Berlin, Heidelberg: Springer. https://doi.org/10.1007/978-3-642-79354-7_2

Bonan, G. B. (2008). Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science*, *320*(5882), 1444–1449. https://doi.org/10.1126/science.1155121

Breiman, L., Friedman, J. H., Olshen, R. A., Stone, C. J. W., & Brooks. C. S. S. (1984). *Classification and regression trees*, *Cole Statistics/Probability Series*. Boca Raton, FL: CRC Press.

Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., et al. (2005). Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(42), 15,144–15,148. https://doi.org/10.1073/pnas.0505734102

Chen, B. Z., Black, T. A., Coops, N. C., Hilker, T., Trofymow, J. A., & Morgenstern, K. (2009). Assessing tower flux footprint climatology and scaling between remotely sensed and Eddy covariance measurements. *Boundary-Layer Meteorology*, *130*(2), 137–167. https://doi.org/10.1007/s10546-008-9339-1

Cheng, Y. B., Middleton, E. M., Zhang, Q., Huemmrich, K. F., Campbell, P. K. E., Corp, L. A., et al. (2013). Integrating solar induced fluorescence and the photochemical reflectance index for estimating gross primary production in a cornfield. *Remote Sensing*, *5*(12), 6857–6879. https://doi.org/10.3390/rs5126857

Collatz, G. J., Ball, J. T., Grivet, C., & Berry, J. A. (1991). Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration-a model that includes laminar boundary-layer. *Agricultural and Forest Meteorology*, *54*(2–4), 107–136. https://doi.org/10.1016/0168-1923(91)90002-8

Demmig-Adams, B., & Adams, W. W. (1992). Photoprotection and other responses of plants to high light stress. *Annual Review of Plant Physiology and Plant Molecular Biology*, *43*(1), 599–626. https://doi.org/10.1146/annurev.pp.43.060192.003123

Demmig-Adams, B., & Adams, W. W. (1996). The role of xanthophyll cycle carotenoids in the protection of photosynthesis. *Trends in Plant Science*, *1*(1), 21–26. https://doi.org/10.1016/s1360-1385(96)80019-7

Demmig-Adams, B., & Adams, W. W. (2000). Photosynthesis: Harvesting sunlight safely. *Nature*, *403*(6768), 371–373. https://doi.org/10.1038/3500031

Demmig-Adams, B., & Adams, W. W. (2006). Photoprotection in an ecological context: the remarkable complexity of thermal energy dissipation. *New Phytologist*, *172*(1), 11–21. https://doi.org/10.1111/j.1469-8137.2006.01835.x

Demmig-Adams, B., Cohu, C. M., Muller, O., & Adams, W. W. (2012). Modulation of photosynthetic energy conversion efficiency in nature: From seconds to seasons. *Photosynthesis Research*, *113*(1–3), 75–88. https://doi.org/10.1007/s11120-012-9761-6

Desai, A. R., Moore, D. J. P., Ahue, W. K. M., Wilkes, P. T. V., De Wekker, S. F. J., Brooks, B. G., et al. (2011). Seasonal pattern of regional carbon balance in the central Rocky Mountains from surface and airborne measurements. *Journal of Geophysical Research*, *116*, G04009. https://doi.org/10.1029/2011JG001655

Dobrowski, S. Z., Pushnik, J. C., Zarco-Tejada, P. J., & Ustin, S. L. (2005). Simple reflectance indices track heat and water stress-induced changes in steady-state chlorophyll fluorescence at the canopy scale. *Remote Sensing of Environment*, *97*(3), 403–414. https://doi.org/10.1016/j.rse.2005.05.006

Drusch, M., Moreno, J., Del Bello, U., Franco, R., Goulas, Y., Kraft, S., et al. (2017). The FLuorescence EXplorer mission concept-ESA's Earth Explorer 8. *IEEE Transactions on Geoscience and Remote Sensing*, *55*(3), 1273–1284. https://doi.org/10.1109/tgrs.2016.2621820

Eitel, J. U. H., Maguire, A. J., Boelman, N., Vierling, L. A., Griffin, K. L., Jensen, J., et al. (2019). Proximal remote sensing of tree physiology at northern treeline: Do late-season changes in the photochemical reflectance index (PRI) respond to climate or photoperiod? *Remote Sensing of Environment*, *221*, 340–350. https://doi.org/10.1016/j.rse.2018.11.022

Ensminger, I., Sveshnikov, D., Campbell, D. A., Funk, C., Jansson, S., Lloyd, J., et al. (2004). Intermittent low temperatures constrain spring recovery of photosynthesis in boreal scots pine forests. *Global Change Biology*, *10*(6), 995–1008. https://doi.org/10.1111/j.1365-2486.2004.00781.x

Evain, S., Flexas, J., & Moya, I. (2004). A new instrument for passive remote sensing: 2. Measurement of leaf and canopy reflectance changes at 531 nm and their relationship with photosynthesis and chlorophyll fluorescence. *Remote Sensing of Environment*, *91*(2), 175–185. https://doi.org/10.1016/j.rse.2004.03.012

Field, C. B. (1991). Ecological scaling of carbon gain to stress and resource availability. In H. A. Mooney, S. E. Winner, E. J. Pell (Eds.), *Response of plants to multiple stresses* (Vol. 28, pp. 35–65). San Diego, CA: Academic Press.

Field, C. B., Randerson, J. T., & Malmström, C. M. (1995). Global net primary production: Combining ecology and remote sensing. *Remote Sensing of Environment*, *51*(1), 74–88. https://doi.org/10.1016/0034-4257(94)00066-V

Filella, I., Penuelas, J., Llorens, L., & Estiarte, M. (2004). Reflectance assessment of seasonal and annual changes in biomass and CO2 uptake of a Mediterranean shrubland submitted to experimental warming and drought. *Remote Sensing of Environment*, *90*(3), 308–318. https://doi.org/10.1016/j.rse.2004.01.010

Filella, I., Porcar-Castell, A., Munne-Bosch, S., Back, J., Garbulsky, M. F., & Penuelas, J. (2009). PRI assessment of long-term changes in carotenoids/chlorophyll ratio and short-term changes in de-epoxidation state of the xanthophyll cycle. *International Journal of Remote Sensing*, *30*(17), 4443–4455. https://doi.org/10.1080/01431160802575661

Flexas, J., Bota, J., Loreto, F., Cornic, G., & Sharkey, T. D. (2004). Diffusive and metabolic limitations to photosynthesis under drought and salinity in C3 plants. *Plant Biology*, *6*(03), 269–279. https://doi.org/10.1055/s-2004-820867

Frechette, E., Chang, C. Y. Y., & Ensminger, I. (2016). Photoperiod and temperature constraints on the relationship between the photochemical reflectance index and the light use efficiency of photosynthesis in *Pinus strobus*. *Tree Physiology*, *36*(3), 311–324. https://doi.org/10.1093/treephys/tpv143

Frechette, E., Wong, C. Y. S., Junker, L. V., Chang, C. Y. Y., & Ensminger, I. (2015). Zeaxanthin-independent energy quenching and alternative electron sinks cause a decoupling of the relationship between the photochemical reflectance index (PRI) and photosynthesis in an evergreen conifer during spring. *Journal of Experimental Botany*, *66*(22), 7309–7323. https://doi.org/10.1093/jxb/erv427

Gamon, J. A. (1993). The dynamic 531-nanometer a reflectance siqnal: A survey of twenty angiosperm species. *Gilmore Hall 202-3050 Maile Way Honolulu*, Hawaii 96822 Office of the Director August *26*, 1993, 172.

Gamon, J. A. (2015). Reviews and syntheses: Optical sampling of the flux tower footprint. *Biogeosciences*, *12*(14), 4509–4523. https://doi.org/10.5194/bg-12-4509-2015

Gamon, J. A., & Berry, J. A. (2012). Facultative and constitutive pigment effects on the photochemical reflectance index (PRI) in sun and shade conifer needles. *Israel Journal of Plant Sciences*, *60*(1–2), 85–95. https://doi.org/10.1560/IJPS.60.1-2.85

Gamon, J. A., & Bond, B. (2013). Effects of irradiance and photosynthetic downregulation on the photochemical reflectance index in Douglas-fir and ponderosa pine. *Remote Sensing of Environment*, *135*, 141–149. https://doi.org/10.1016/j.rse.2013.03.032

Gamon, J. A., Coburn, C., Flanagan, L. B., Huemmrich, K. F., Kiddle, C., Sanchez-Azofeifa, G. A., et al. (2010). SpecNet revisited: Bridging flux and remote sensing communities. *Canadian Journal of Remote Sensing*, *36*(sup2), S376–S390. https://doi.org/10.5589/m10-067

Gamon, J. A., Field, C. B., Goulden, M. L., Griffin, K. L., Hartley, A. E., Joel, G., et al. (1995). Relationships between NDVI, canopy structure, and photosynthesis in three Californian vegetation types. *Ecological Applications*, *5*(1), 28–41. https://doi.org/10.2307/1942049

Gamon, J. A., Huemmrich, K. F., Wong, C. Y., Ensminger, I., Garrity, S., Hollinger, D. Y., et al. (2016). A remotely sensed pigment index reveals photosynthetic phenology in evergreen conifers. *Proceedings of the National Academy of Sciences*, *113*(46), 13,087–13,092. https://doi.org/10.1073/pnas.1606162113

Gamon, J. A., Kovalchuck, O., Wong, C. Y. S., Harris, A., & Garrity, S. R. (2015). Monitoring seasonal and diurnal changes in photosynthetic pigments with automated PRI and NDVI sensors. *Biogeosciences*, *12*(13), 4149–4159. https://doi.org/10.5194/bg-12-4149-2015

Gamon, J. A., Peñuelas, J., & Field, C. B. (1992). A narrow-waveband spectral index that tracks diurnal changes in photosynthetic efficiency. *Remote Sensing of Environment*, *41*(1), 35–44. https://doi.org/10.1016/0034-4257(92)90059-S

Gamon, J. A., Rahman, A. F., Dungan, J. L., Schildhauer, M., & Huemmrich, K. F. (2006). Spectral network (SpecNet)—What is it and why do we need it? *Remote Sensing of Environment*, *103*(3), 227–235. https://doi.org/10.1016/j.rse.2006.04.003

Gamon, J. A., Serrano, L., & Surfus, J. S. (1997). The photochemical reflectance index: An optical indicator of photosynthetic radiation use efficiency across species, functional types, and nutrient levels. *Oecologia*, *112*(4), 492–501. https://doi.org/10.1007/s004420050337

Gamon, J. A., & Surfus, J. S. (1999). Assessing leaf pigment content and activity with a reflectometer. *New Phytologist*, *143*(1), 105–117. https://doi.org/10.1046/j.1469-8137.1999.00424.x

Garbulsky, M. F., Peñuelas, J., Gamon, J., Inoue, Y., & Filella, I. (2011). The photochemical reflectance index (PRI) and the remote sensing of leaf, canopy and ecosystem radiation use efficiencies: A review and meta-analysis. *Remote Sensing of Environment*, *115*(2), 281–297. https://doi.org/10.1016/j.rse.2010.08.023

Garrity, S. R., Eitel, J. U. H., & Vierling, L. A. (2011). Disentangling the relationships between plant pigments and the photochemical reflectance index reveals a new approach for remote estimation of carotenoid content. *Remote Sensing of Environment*, *115*(2), 628–635. https://doi.org/10.1016/j.rse.2010.10.007

Genty, B., Briantais, J. M., & Baker, N. R. (1989). The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochimica et Biophysica Acta (BBA) - General Subjects*, *990*(1), 87–92. https://doi.org/10.1016/S0304-4165(89)80016-9

Gitelson, A. A., Gamon, J. A., & Solovchenko, A. (2017). Multiple drivers of seasonal change in PRI: Implications for photosynthesis 1. Leaf level. *Remote Sensing of Environment*, *191*, 110–116. https://doi.org/10.1016/j.rse.2016.12.014

Grace, J., Nichol, C., Disney, M., Lewis, P., Quaife, T., & Bowyer, P. (2007). Can we measure terrestrial photosynthesis from space directly, using spectral reflectance and fluorescence? *Global Change Biology*, *13*, 1484–1497. https://doi.org/10.1111/j.1365-2486.2007.01352.x

Granier, A. (1985). Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. *Annales des Sciences Forestières*, *42*(2), 193–200. https://doi.org/10.1051/forest:19850204

Granier, A. (1987). Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiology*, *3*(4), 309–320. https://doi.org/10.1093/treephys/3.4.309

Guarini, R., Nichol, C., Clement, R., Loizzo, R., Grace, J., & Borghetti, M. (2014). The utility of MODIS-sPRI for investigating the photosynthetic light-use efficiency in a Mediterranean deciduous forest. *International Journal of Remote Sensing*, *35*(16), 6157–6172. https://doi.org/10.1080/01431161.2014.950762

Guo, J. M., & Trotter, C. M. (2004). Estimating photosynthetic light-use efficiency using the photochemical reflectance index: Variations among species. *Functional Plant Biology*, *31*(3), 255–265. https://doi.org/10.1071/fp03185

Haldimann, P., Gallé, A., & Feller, U. (2008). Impact of an exceptionally hot dry summer on photosynthetic traits in oak (Quercus pubescens) leaves. *Tree Physiology*, *28*(5), 785–795. https://doi.org/10.1093/treephys/28.5.785

Hall, F. G., Hilker, T., Coops, N. C., Lyapustin, A., Huemmrich, K. F., Middleton, E., et al. (2008). Multi-angle remote sensing of forest light use efficiency by observing PRI variation with canopy shadow fraction. *Remote Sensing of Environment*, *112*(7), 3201–3211. https://doi.org/10.1016/j.rse.2008.03.015

Harbinson, J., Genty, B., & Baker, N. R. (1990). The relationship between CO_2 assimilation and electron transport in leaves. *Photosynthesis Research*, *25*(3), 213–224. https://doi.org/10.1007/BF00033162

He, M., Kimball, J. S., Running, S., Ballantyne, A., Guan, K., & Huemmrich, F. (2016). Satellite detection of soil moisture related water stress impacts on ecosystem productivity using the MODIS-based photochemical reflectance index. *Remote Sensing of Environment*, *186*(Supplement C), 173–183. https://doi.org/10.1016/j.rse.2016.08.019

Hernandez-Clemente, R., Kolari, P., Porcar-Castell, A., Korhonen, L., & Mottus, M. (2016). Tracking the seasonal dynamics of boreal forest photosynthesis using EO-1 hyperion reflectance: Sensitivity to structural and illumination effects. *IEEE Transactions on Geoscience and Remote Sensing*, *54*(9), 5105–5116. https://doi.org/10.1109/tgrs.2016.2554466

Hernandez-Clemente, R., Navarro-Cerrillo, R. M., Suarez, L., Morales, F., & Zarco-Tejada, P. J. (2011). Assessing structural effects on PRI for stress detection in conifer forests. *Remote Sensing of Environment*, *115*(9), 2360–2375. https://doi.org/10.1016/j.rse.2011.04.036

Hilker, T., Coops, N. C., Hall, F. G., Black, T. A., Wulder, M. A., Nesic, Z., & Krishnan, P. (2008). Separating physiologically and directionally induced changes in PRI using BRDF models. *Remote Sensing of Environment*, *112*(6), 2777–2788. https://doi.org/10.1016/j.rse.2008.01.011

Hilker, T., Hall, F. G., Coops, N. C., Collatz, J. G., Black, T. A., Tucker, C. J., et al. (2013). Remote sensing of transpiration and heat fluxes using multi-angle observations. *Remote Sensing of Environment*, *137*, 31–42. https://doi.org/10.1016/j.rse.2013.05.023

Hilker, T., Nesic, Z., Coops, N. C., & Lessard, D. (2010). A new, automated, multiangular radiometer instrument for tower-based observations of canopy reflectance (amspec ii). *Instrumentation Science & Technology*, *38*(5), 319–340. https://doi.org/10.1080/10739149.2010.508357

Hmimina, G., Dufrene, E., & Soudani, K. (2014). Relationship between photochemical reflectance index and leaf ecophysiological and biochemical parameters under two different water statuses: Towards a rapid and efficient correction method using real-time measurements. *Plant, Cell & Environment*, *37*(2), 473–487. https://doi.org/10.1111/pce.12171

Hmimina, G., Merlier, E., Dufrene, E., & Soudani, K. (2015). Deconvolution of pigment and physiologically related photochemical reflectance index variability at the canopy scale over an entire growing season. *Plant, Cell & Environment*, *38*(8), 1578–1590. https://doi.org/10.1111/pce.12509

Huxman, T. E., Snyder, K. A., Tissue, D., Leffler, A. J., Ogle, K., Pockman, W. T., et al. (2004). Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia*, *141*(2), 254–268. https://doi.org/10.1007/s00442-004-1682-4

Inoue, Y., & Penuelas, J. (2006). Relationship between light use efficiency and photochemical reflectance index in soybean leaves as affected by soil water content. *International Journal of Remote Sensing*, *27*(22), 5109–5114. https://doi.org/10.1080/01431160500373039

Jahns, P., & Holzwarth, A. R. (2012). The role of the xanthophyll cycle and of lutein in photoprotection of photosystem II. *Biochimica et Biophysica Acta (BBA)-Bioenergetics*, *1817*(1), 182–193. https://doi.org/10.1016/j.bbabio.2011.04.012

Jia, W., Coops, N. C., Tortini, R., Pang, Y., & Black, T. A. (2018). Remote sensing of variation of light use efficiency in two age classes of Douglas-fir. *Remote Sensing of Environment*, *219*, 284–297. https://doi.org/10.1016/j.rse.2018.10.017

Jung, M., Reichstein, M., Margolis, H. A., Cescatti, A., Richardson, A. D., Arain, M. A., et al. (2011). Global patterns of land-atmosphere fluxes of carbon dioxide, latent heat, and sensible heat derived from eddy covariance, satellite, and meteorological observations. *Journal of Geophysical Research*, *116*, G00J07. https://doi.org/10.1029/2010JG001566

Knowles, J. F., Scott, R. L., Minor, R. L., & Barron-Gafford, G. A. (2020). Ecosystem carbon and water cycling from a sky island montane forest. *Agricultural and Forest Meteorology*, *281*, 107835. https://doi.org/10.1016/j.agrformet.2019.107835

Lasslop, G., Reichstein, M., Papale, D., Richardson, A., Arneth, A., Barr, A., et al. (2010). Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: Critical issues and global evaluation. *Global Change Biology*, *16*(1), 187–208. https://doi.org/10.1111/j.1365-2486.2009.02041.x

Long, S. P., & Bernacchi, C. J. (2003). Gas exchange measurements, what can they tell us about the underlying limitations to photosynthesis? Procedures and sources of error. *Journal of Experimental Botany*, *54*(392), 2393–2401. https://doi.org/10.1093/jxb/erg262

Loriaux, S. D., Avenson, T. J., Welles, J. M., McDermitt, D. K., Eckles, R. D., Riensche, B., & Genty, B. (2013). Closing in on maximum yield of chlorophyll fluorescence using a single multiphase flash of sub-saturating intensity. *Plant, Cell & Environment*, *36*(10), 1755–1770. https://doi.org/10.1111/pce.12115

Louis, J., Ounis, A., Ducruet, J. M., Evain, S., Laurila, T., Thum, T., et al. (2005). Remote sensing of sunlight-induced chlorophyll fluorescence and reflectance of scots pine in the boreal forest during spring recovery. *Remote Sensing of Environment*, *96*(1), 37–48. https://doi.org/10.1016/j.rse.2005.01.013

Magney, T. S., Bowling, D. R., Logan, B. A., Grossmann, K., Stutz, J., Blanken, P. D., et al. (2019). Mechanistic evidence for tracking the seasonality of photosynthesis with solar-induced fluorescence. *Proceedings of the National Academy of Sciences*, *116*(24), 11,640–11,645. https://doi.org/10.1073/pnas.1900278116

Magney, T. S., Vierling, L. A., Eitel, J. U. H., Huggins, D. R., & Garrity, S. R. (2016). Response of high frequency photochemical reflectance index (PRI) measurements to environmental conditions in wheat. *Remote Sensing of Environment*, *173*, 84–97. https://doi.org/10.1016/j.rse.2015.11.013

Manzanera, J. A., Gomez-Garay, A., Pintos, B., Rodriguez-Rastrero, M., Moreda, E., Zazo, J., et al. (2017). Sap flow, leaf-level gas exchange and spectral responses to drought in *Pinus sylvestris*, *Pinus pinea* and *Pinus halepensis*. *Iforest-Biogeosciences and Forestry*, *10*(1), 204–214. https://doi.org/10.3832/ifor1748-009

Marino, G., Pallozzi, E., Cocozza, C., Tognetti, R., Giovannelli, A., Cantini, C., & Centritto, M. (2014). Assessing gas exchange, sap flow and water relations using tree canopy spectral reflectance indices in irrigated and rainfed *Olea europaea* L. *Environmental and Experimental Botany*, *99*, 43–52. https://doi.org/10.1016/j.envexpbot.2013.10.008

Meinzer, F. C. (2002). Co-ordination of vapour and liquid phase water transport properties in plants. *Plant, Cell & Environment*, *25*(2), 265–274. https://doi.org/10.1046/j.1365-3040.2002.00781.x

Merlier, E., Hmimina, G., Dufrêne, E., & Soudani, K. (2015). Explaining the variability of the photochemical reflectance index (PRI) at the canopy-scale: Disentangling the effects of phenological and physiological changes. *Journal of Photochemistry and Photobiology B: Biology*, *151*, 161–171. https://doi.org/10.1016/j.jphotobiol.2015.08.006

Middleton, E. M., Cheng, Y. B., Hilker, T., Black, T. A., Krishnan, P., Coops, N. C., & Huemmrich, K. F. (2009). Linking foliage spectral responses to canopy-level ecosystem photosynthetic light-use efficiency at a Douglas-fir forest in Canada. *Canadian Journal of Remote Sensing*, *35*(2), 166–188. https://doi.org/10.5589/m09-008

Monson, R. K., Turnipseed, A. A., Sparks, J. P., Harley, P. C., Scott-Denton, L. E., Sparks, K., & Huxman, T. E. (2002). Carbon sequestration in a high-elevation, subalpine forest. *Global Change Biology*, *8*, 459–478. https://doi.org/10.1046/j.1365-2486.2002.00480.x

Mottus, M., Takala, T. L. H., Stenberg, P., Knyazikhin, Y., Yang, B., & Nilson, T. (2015). Diffuse sky radiation influences the relationship between canopy PRI and shadow fraction. *ISPRS Journal of Photogrammetry and Remote Sensing*, *105*, 54–60. https://doi.org/10.1016/j.isprsjprs.2015.03.012

Muller, P., Li, X. P., & Niyogi, K. K. (2001). Non-photochemical quenching. A response to excess light energy. *Plant Physiology*, *125*(4), 1558–1566. https://doi.org/10.1104/pp.125.4.1558

Myneni, R. B., & Williams, D. L. (1994). On the relationship between fAPAR and NDVI. *Remote Sensing of Environment*, *49*(3), 200–211. https://doi.org/10.1016/0034-4257(94)90016-7

Nakaji, T., Kosugi, Y., Takanashi, S., Niiyama, K., Noguchi, S., Tani, M., et al. (2014). Estimation of light-use efficiency through a combinational use of the photochemical reflectance index and vapor pressure deficit in an evergreen tropical rainforest at Pasoh, peninsular Malaysia. *Remote Sensing of Environment*, *150*, 82–92. https://doi.org/10.1016/j.rse.2014.04.021

Nakaji, T., Oguma, H., & Fujinuma, Y. (2006). Seasonal changes in the relationship between photochemical reflectance index and photosynthetic light use efficiency of Japanese larch needles. *International Journal of Remote Sensing*, *27*(3), 493–509. https://doi.org/10.1080/01431160500329528

Naumann, J. C., Bissett, S. N., Young, D. R., Edwards, J., & Anderson, J. E. (2010). Diurnal patterns of photosynthesis, chlorophyll fluorescence, and PRI to evaluate water stress in the invasive species, *Elaeagnus umbellata* Thunb. *Trees*, *24*(2), 237–245. https://doi.org/10.1007/s00468-009-0394-0

Nestola, E., Scartazza, A., Di Baccio, D., Castagna, A., Ranieri, A., Cammarano, M., et al. (2018). Are optical indices good proxies of seasonal changes in carbon fluxes and stress-related physiological status in a beech forest? *Science of the Total Environment*, *612*, 1030–1041. https://doi.org/10.1016/j.scitotenv.2017.08.167

Nichol, C. J., Lloyd, J., Shibistova, O., Arneth, A., Roser, C., Knohl, A., et al. (2002). Remote sensing of photosynthetic-light-use efficiency of a Siberian boreal forest. *Tellus Series B: Chemical and Physical Meteorology*, *54*(5), 677–687. https://doi.org/10.3402/tellusb.v54i5.16710

Pacheco-Labrador, J., El-Madany, T. S., Martin, M. P., Migliavacca, M., Rossini, M., Carrara, A., & Zarco-Tejada, P. J. (2017). Spatio-temporal relationships between optical information and carbon fluxes in a Mediterranean tree-grass ecosystem. *Remote Sensing*, *9*(6), 25. https://doi.org/10.3390/rs9060608

Papageorgiou, G. C., & Govindjee (2014). The non-photochemical quenching of the electronically excited state of chlorophyll a in plants: Definitions, timelines, viewpoints, open questions. In B. Demmig-Adams, G. Garab, W. Adams, III, Govindjee (Eds.), *Non-Photochemical Quenching and Energy Dissipation in Plants, Algae and Cyanobacteria* (Vol. 40, pp. 1–44). Dordrecht: Springer. https://doi.org/10.1007/978-94-017-9032-1_1

Penuelas, J., Filella, I., & Gamon, J. A. (1995). Assessment of photosynthetic radiation-use efficiency with spectral reflectance. *New Phytologist*, *131*(3), 291–296. https://doi.org/10.1111/j.1469-8137.1995.tb03064.x

Penuelas, J., Filella, I., Llusia, J., Siscart, D., & Pinol, J. (1998). Comparative field study of spring and summer leaf gas exchange and photobiology of the Mediterranean trees *Quercus ilex* and *Phillyrea latifolia*. *Journal of Experimental Botany*, *49*(319), 229–238. https://doi.org/10.1093/jexbot/49.319.229

Porcar-Castell, A. (2011). A high-resolution portrait of the annual dynamics of photochemical and non-photochemical quenching in needles of *Pinus sylvestris*. *Physiologia Plantarum*, *143*(2), 139–153. https://doi.org/10.1111/j.1399-3054.2011.01488.x

Porcar-Castell, A., Garcia-Plazaola, J. I., Nichol, C. J., Kolari, P., Olascoaga, B., Kuusinen, N., et al. (2012). Physiology of the seasonal relationship between the photochemical reflectance index and photosynthetic light use efficiency. *Oecologia*, *170*(2), 313–323. https://doi.org/10.1007/s00442-012-2317-9

Potts, D. L., Minor, R. L., Braun, Z., & Barron-Gafford, G. A. (2017). Photosynthetic phenological variation may promote coexistence among co-dominant tree species in a Madrean sky island mixed conifer forest. *Tree Physiology*, *37*(9), 1229–1238. https://doi.org/10.1093/treephys/tpx076

Prince, S. D., & Goward, S. N. (1995). Global primary production: A remote sensing approach. *Journal of Biogeography*, *22*(4–5), 815–835. https://doi.org/10.2307/2845983

Rahimzadeh-Bajgiran, P., Munehiro, M., & Omasa, K. (2012). Relationships between the photochemical reflectance index (PRI) and chlorophyll fluorescence parameters and plant pigment indices at different leaf growth stages. *Photosynthesis Research*, *113*(1–3), 261–271. https://doi.org/10.1007/s11120-012-9747-4

Ripullone, F., Rivelli, A. R., Baraldi, R., Guarini, R., Guerrieri, R., Magnani, F., et al. (2011). Effectiveness of the photochemical reflectance index to track photosynthetic activity over a range of forest tree species and plant water statuses. *Functional Plant Biology*, *38*(3), 177–186. https://doi.org/10.1071/fp10078

Rossini, M., Fava, F., Cogliati, S., Meroni, M., Marchesi, A., Panigada, C., et al. (2013). Assessing canopy PRI from airborne imagery to map water stress in maize. *ISPRS Journal of Photogrammetry and Remote Sensing*, *86*, 168–177. https://doi.org/10.1016/j.isprsjprs.2013.10.002

Running, S. W., Nemani, R. R., Heinsch, F. A., Zhao, M., Reeves, M., & Hashimoto, H. (2004). A continuous satellite-derived measure of global terrestrial primary production. *Bioscience*, *54*(6), 547–560. https://doi.org/10.1641/0006-3568(2004)054[0547:ACSMOG]2.0.CO;2

Sarlikioti, V., Driever, S. M., & Marcelis, L. F. M. (2010). Photochemical reflectance index as a mean of monitoring early water stress. *Annals of Applied Biology*, *157*(1), 81–89. https://doi.org/10.1111/j.1744-7348.2010.00411.x

Schimel, D., Pavlick, R., Fisher, J. B., Asner, G. P., Saatchi, S., Townsend, P., et al. (2015). Observing terrestrial ecosystems and the carbon cycle from space. *Global Change Biology*, *21*(5), 1762–1776. https://doi.org/10.1111/gcb.12822

Schimel, D. T., Kittel, G. F., Running, S., Monson, R., Turnispeed, A., & Anderson, D. (2002). Carbon sequestration studied in western U.S. mountains. *Eos Transactions American Geophysical Union*, *83*(40), 445–449. https://doi.org/10.1029/2002EO000314

Scott, R. L., Biederman, J. A., Hamerlynck, E. P., & Barron-Gafford, G. A. (2015). The carbon balance pivot point of southwestern US semiarid ecosystems: Insights from the 21st century drought. *Journal of Geophysical Research: Biogeosciences*, *120*, 2612–2624. https://doi.org/10.1002/2015JG003181

Seager, R., Ting, M. F., Held, I., Kushnir, Y., Lu, J., Vecchi, G., et al. (2007). Model projections of an imminent transition to a more arid climate in southwestern North America. *Science*, *316*(5828), 1181–1184. https://doi.org/10.1126/science.1139601

Serrano, L., & Penuelas, J. (2005). Assessing forest structure and function from spectral transmittance measurements: A case study in a Mediterranean holm oak forest. *Tree Physiology*, *25*(1), 67–74. https://doi.org/10.1093/treephys/25.1.67

Shiklomanov, A. N., Bradley, B. A., Dahlin, K. M., Fox, A. M., Gough, C. M., Hoffman, F. M., et al. (2019). Enhancing global change experiments through integration of remote-sensing techniques. *Frontiers in Ecology and the Environment*, *17*(4), 215–224. https://doi.org/10.1002/fee.2031

Sims, D. A., & Gamon, J. A. (2002). Relationships between leaf pigment content and spectral reflectance across a wide range of species, leaf structures and developmental stages. *Remote Sensing of Environment*, *81*(2), 337–354. https://doi.org/10.1016/S0034-4257(02)00010-X

Sims, D. A., Luo, H. Y., Hastings, S., Oechel, W. C., Rahman, A. F., & Gamon, J. A. (2006). Parallel adjustments in vegetation greenness and ecosystem CO_2 exchange in response to drought in a Southern California chaparral ecosystem. *Remote Sensing of Environment*, *103*(3), 289–303. https://doi.org/10.1016/j.rse.2005.01.020

Sims, D. A., Rahman, A. F., Cordova, V. D., Baldocchi, D. D., Flanagan, L. B., Goldstein, A. H., et al. (2005). Midday values of gross CO_2 flux and light use efficiency during satellite overpasses can be used to directly estimate eight-day mean flux. *Agricultural and Forest Meteorology*, *131*(1–2), 1–12. https://doi.org/10.1016/j.agrformet.2005.04.006

Smith, W. K., Biederman, J. A., Scott, R. L., Moore, D. J. P., He, M., Kimball, J. S., et al. (2018). Chlorophyll fluorescence better captures seasonal and interannual gross primary productivity dynamics across dryland ecosystems of Southwestern North America. *Geophysical Research Letters*, *45*, 748–757. https://doi.org/10.1002/2017GL075922

Smith, W. K., Dannenberg, M. P., Yan, D., Herrmann, S., Barnes, M. L., Barron-Gafford, G. A., et al. (2019). Remote sensing of dryland ecosystem structure and function: Progress, challenges, and opportunities. *Remote Sensing of Environment*, *233*, 111401. https://doi.org/10.1016/j.rse.2019.111401

Smith, W. K., Reed, S. C., Cleveland, C. C., Ballantyne, A. P., Anderegg, W. R. L., Wieder, W. R., et al. (2016). Large divergence of satellite and earth system model estimates of global terrestrial CO_2 fertilization. *Nature Climate Change*, *6*(3), 306–310. https://doi.org/10.1038/nclimate2879

Soudani, K., Hmimina, G., Dufrene, E., Berveiller, D., Delpierre, N., Ourcival, J. M., et al. (2014). Relationships between photochemical reflectance index and light-use efficiency in deciduous and evergreen broadleaf forests. *Remote Sensing of Environment*, *144*, 73–84. https://doi.org/10.1016/j.rse.2014.01.017

Stylinski, C. D., Gamon, J. A., & Oechel, W. C. (2002). Seasonal patterns of reflectance indices, carotenoid pigments and photosynthesis of evergreen chaparral species. *Oecologia*, *131*(3), 366–374. https://doi.org/10.1007/s00442-002-0905-9

Suarez, L., Zarco-Tejada, P. J., Sepulcre-Canto, G., Perez-Priego, O., Miller, J. R., Jimenez-Munoz, J. C., & Sobrino, J. (2008). Assessing canopy PRI for water stress detection with diurnal airborne imagery. *Remote Sensing of Environment*, *112*(2), 560–575. https://doi.org/10.1016/j.rse.2007.05.009

Sun, P. S., Wahbi, S., Tsonev, T., Haworth, M., Liu, S. R., & Centritto, M. (2014). On the use of leaf spectral indices to assess water status and photosynthetic limitations in *Olea europaea* L. during water-stress and recovery. *PLoS ONE*, *9*(8), 12. https://doi.org/10.1371/journal.pone.0105165

Thenot, F., Methy, M., & Winkel, T. (2002). The photochemical reflectance index (PRI) as a water-stress index. *International Journal of Remote Sensing*, *23*(23), 5135–5139. https://doi.org/10.1080/01431160210163100

Tsonev, T., Wahbi, S., Sun, P. S., Sorrentino, G., & Centritto, M. (2014). Gas exchange, water relations and their relationships with photochemical reflectance index in Quercus ilex plants during water stress and recovery. *International Journal of Agriculture and Biology*, *16*(2), 335–341.

Udall, B., & Overpeck, J. (2017). The twenty-first century Colorado River hot drought and implications for the future. *Water Resources Research*, *53*, 2404–2418. https://doi.org/10.1002/2016WR019638

Verhoeven, A. (2014). Sustained energy dissipation in winter evergreens. *New Phytologist*, *201*(1), 57–65. https://doi.org/10.1111/nph.12466

Verma, M., Schimel, D., Evans, B., Frankenberg, C., Beringer, J., Drewry, D. T., et al. (2017). Effect of environmental conditions on the relationship between solar-induced fluorescence and gross primary productivity at an OzFlux grassland site. *Journal of Geophysical Research: Biogeosciences*, *122*, 716–733. https://doi.org/10.1002/2016JG003580

Walther, S., Voigt, M., Thum, T., Gonsamo, A., Zhang, Y. G., Kohler, P., et al. (2016). Satellite chlorophyll fluorescence measurements reveal large-scale decoupling of photosynthesis and greenness dynamics in boreal evergreen forests. *Global Change Biology*, *22*(9), 2979–2996. https://doi.org/10.1111/gcb.13200

Williams, A. P., Allen, C. D., Macalady, A. K., Griffin, D., Woodhouse, C. A., Meko, D. M., et al. (2013). Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*, *3*(3), 292–297. https://doi.org/10.1038/nclimate1693

Wong, C. Y., D'Odorico, P., Arain, M. A., & Ensminger, I. (2020). Tracking the phenology of photosynthesis using carotenoid-sensitive and near-infrared reflectance vegetation indices in a temperate evergreen and mixed deciduous forest. *New Phytologist*. https://doi.org/10.1111/nph.16479

Wong, C. Y. S., D'Odorico, P., Bhathena, Y., Arain, M. A., & Ensminger, I. (2019). Carotenoid based vegetation indices for accurate monitoring of the phenology of photosynthesis at the leaf-scale in deciduous and evergreen trees. *Remote Sensing of Environment*, *233*, 111,407. https://doi.org/10.1016/j.rse.2019.111407

Wong, C. Y. S., & Gamon, J. A. (2015a). The photochemical reflectance index provides an optical indicator of spring photosynthetic activation in evergreen conifers. *New Phytologist*, *206*(1), 196–208. https://doi.org/10.1111/nph.13251

Wong, C. Y. S., & Gamon, J. A. (2015b). Three causes of variation in the photochemical reflectance index (PRI) in evergreen conifers. *New Phytologist*, *206*(1), 187–195. https://doi.org/10.1111/nph.13159

Zarco-Tejada, P. J., Gonzalez-Dugo, V., & Berni, J. A. J. (2012). Fluorescence, temperature and narrow-band indices acquired from a UAV platform for water stress detection using a micro-hyperspectral imager and a thermal camera. *Remote Sensing of Environment*, *117*, 322–337. https://doi.org/10.1016/j.rse.2011.10.007

Zarco-Tejada, P. J., González-Dugo, V., Williams, L. E., Suárez, L., Berni, J. A. J., Goldhamer, D., & Fereres, E. (2013). A PRI-based water stress index combining structural and chlorophyll effects: Assessment using diurnal narrow-band airborne imagery and the CWSI thermal index. *Remote Sensing of Environment*, *138*, 38–50. https://doi.org/10.1016/j.rse.2013.07.024

Zhang, C., Filella, I., Garbulsky, M. F., & Penuelas, J. (2016). Affecting factors and recent improvements of the photochemical reflectance index (PRI) for remotely sensing foliar, canopy and ecosystemic radiation-use efficiencies. *Remote Sensing*, *8*(9), 33. https://doi.org/10.3390/rs8090677

Zhang, C., Filella, I., Liu, D., Ogaya, R., Llusià, J., Asensio, D., & Peñuelas, J. (2017). Photochemical reflectance index (PRI) for detecting responses of diurnal and seasonal photosynthetic activity to experimental drought and warming in a Mediterranean shrubland. *Remote Sensing*, *9*(11), 1189. https://doi.org/10.3390/rs9111189

Zhang, Q., Ju, W. M., Chen, J. M., Wang, H. M., Yang, F. T., Fan, W. L., et al. (2015). Ability of the photochemical reflectance index to track light use efficiency for a sub-tropical planted coniferous forest. *Remote Sensing*, *7*(12), 16,938–16,962. https://doi.org/10.3390/rs71215860

Zuromski, L. M., Bowling, D. R., Köhler, P., Frankenberg, C., Goulden, M. L., Blanken, P. D., & Lin, J. C. (2018). Solar-induced fluorescence detects interannual variation in gross primary production of coniferous forests in the Western United States. *Geophysical Research Letters*, *45*, 7184–7193. https://doi.org/10.1029/2018GL077906